

Biology and Ecology of Flower Thrips in Relation to *Tomato Spotted Wilt Virus**

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Abstract

Tomato Spotted Wilt Virus (TSWV) is transmitted exclusively by certain species of thrips. Because TSWV can only be acquired by larvae and transmitted by adults, it is essential to determine the ecology of these different life stages to improve management of thrips and TSWV. Furthermore, interspecific differences among vector species complicate management issues. Herein, aspects of the biology and ecology of thrips vectors of tomato spotted wilt virus are discussed and an overview of vector-pathogens interaction is given. The complex of native and adventive *Frankliniella* species that occur in the southeastern USA is used as a model system for comparing and contrasting species-specific behavioral attributes that affect large-scale spatial and temporal population dynamics. The common *Frankliniella* species in the southeastern USA include *Frankliniella occidentalis*, *F. fusca*, *F. bispinosa*, and *F. tritici*. The western flower thrips, *F. occidentalis*, is considered the predominant vector of TSWV, but *F. bispinosa* and *F. fusca* are also vectors. These *Frankliniella* species have rapid generation times, and adults are highly polyphagous. Numerous hosts may serve as sources for thrips entering tomato fields, yet tomato is a poor reproductive host. Therefore, most of the thrips infesting fields are immigrants. Consequently, thrips dispersal behavior is a key component of TSWV epidemiology. *F. occidentalis* is a less mobile species than either *F. bispinosa* or *F. tritici*. These interspecific differences in the activity levels of adults affect how the species colonize plants and the field efficacy of insecticides against each species. These results show the importance of understanding interspecific variation among vectors for management of TSWV.

INTRODUCTION

Tomato Spotted Wilt Virus (TSWV) is one of the most severe problems facing vegetable and ornamental production worldwide (Goldbach and Peters, 1994; Moyer et al., 1999). Tomato spotted wilt is an especially damaging disease in tomato, *Lycopersicon esculentum*. Infected plants do not produce marketable fruit, although symptoms may not be apparent until after harvest. *Tomato Spotted Wilt Virus*, the type species of the *Tospovirus* genus, is the predominant species, but other species attack tomato (e.g., Nagata et al., 1995). Management of these important plant pathogens is complicated by the behavior and ecology of the thrips that vector it and interspecific variations in those characters among thrips. In this paper, some of the attributes contributing to the pest status of different thrips species are discussed. The complex of native and adventive *Frankliniella* species that occur in the southeastern USA is used as a model system for comparing and contrasting species-specific behavioral attributes that affect large-scale spatial and temporal population dynamics, and interactions with *Tomato Spotted Wilt Virus*.

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DISCUSSION

Thrips Bionomics

Of the more than 5,000 described species of thrips in the world, a relatively small number of species are agricultural pests (Lewis, 1997b; Mound, 1997). From a plant disease perspective, all known vectors of *Tospoviruses* are in only two genera of thrips, *Frankliniella* and *Thrips* (Iwaki et al., 1984; Kobatake et al., 1984; Mound, 1996; Sakimura, 1962; Sakimura, 1963; Ullman et al., 1997; Webb et al., 1997; Y. Avila et al., unpub.). The seeming paucity of recognized vector species within these two large genera may be considered surprising. There are 180 known species of *Frankliniella*, yet only five species, *F. bispinosa*, *F. fusca*, *F. intonsa*, *F. occidentalis*, and *F. schultzei*, are known vectors of *Tospoviruses*. Of the 275 known species of *Thrips* only *T. palmi*, *T. setosus* and *T. tabaci* are known vectors of *Tospoviruses*. All of these species are known pests of tomatoes, and, except for *T. palmi*, are vectors of TSWV. The primary vector of TSWV worldwide is the western flower thrips, *F. occidentalis*, but the others are regionally important as vectors. Although it is not a vector of TSWV, *Thrips palmi*, the melon thrips, is a vector of other *Tospoviruses*, as well as being a serious pest even in the absence of virus transmission (Kajita et al., 1996; Welter et al., 1990).

In the southeastern USA, there is a complex of *Frankliniella* species that infests tomatoes. Three of these species, *F. bispinosa*, *F. fusca* and *F. occidentalis*, are vectors of TSWV, but another common species *F. tritici* is not a vector (Sakimura, 1962). The abundance of *F. tritici* in vegetable crops complicates management issues because it is morphologically similar to *F. bispinosa* and *F. occidentalis*, making it difficult for growers to discern which species may be present in their fields. These species also inhabit a wide variety of wild and cultivated host plants (Chellemi et al., 1994; Puche et al., 1995; Reitz, 2002).

The seasonal dynamics of these species in tomatoes in northern Florida show consistent patterns from year to year. Adult populations are low in the early spring, but build rapidly and peak in mid May. Populations decline just as rapidly and remain low for the rest of the year (Fig. 1; Reitz, 2002; Salguero-Navas et al., 1991). This pattern of rapid increases and declines in abundance is typical of *Frankliniella* species in other crops in other regions of the world (e.g., Davidson and Andrewartha, 1948; Eckel et al., 1996; Hansen et al., 2003; Pearsall and Myers, 2000).

Adult *Frankliniella* females have a saw-like ovipositor, which they use to deposit eggs within plant tissue. Because eggs are within plant tissue, they are relatively protected from many natural enemies as well as insecticides that lack systemic or translaminar properties (Lewis, 1997a). Under laboratory conditions of $26 \pm 1^\circ\text{C}$, 14:10 L:D, eggs of *F. occidentalis* and *F. tritici* hatch in approximately 3 days (Fig. 2). There are two larval feeding stages, followed by two nonfeeding pupal stages. Under laboratory conditions ($26 \pm 1^\circ\text{C}$, 14:10 L:D), *F. occidentalis* and *F. tritici* can complete the larval and pupal stages within nine days (Fig. 2). This rapid development allows multiple, overlapping generations to occur, as evidenced by the continuous presence of adults and immatures throughout the growing season.

Adults and larvae have piercing mouthparts and feed on similar resources. The mandible pierces plant cells, and the thrips drains the liquid, leaving behind necrotic scars (Childers, 1997; Chisholm and Lewis, 1984). This aesthetic damage is a serious concern for ornamental producers. However, the greatest concern is from adult thrips transmitting TSWV or other *Tospoviruses* to vegetables and ornamentals.

Although adult and larval *Frankliniella* thrips feed in a similar manner, all of the plant species that serve as adult feeding hosts may not be suitable hosts for larvae to complete development. Only hosts on which the net reproductive rate is greater than one would be significant sources of thrips. Tomato, especially under commercial production conditions, is not a good reproductive host for *Frankliniella* or *Thrips* spp. (Kawai, 1986; Puche et al., 1995; Reitz, 2002; Stavisky et al., 2002). Comparing the ratio of adults to larvae of *Frankliniella* spp. on tomatoes versus peppers (*Capsicum annuum*) shows that

there are always more adults than larvae on tomato than on pepper (Baez, 2002; Fig. 3). In addition, tomato does not appear to be a preferred host for adults of *Frankliniella* spp. In no choice trials to compare time budgets, *F. occidentalis* females spend more time feeding and more time in residence on pepper than on tomato (Fig. 4; Reitz et al., 2002). Also, *F. occidentalis* females are more prone to move off tomatoes than peppers once they alight. These behavioral data indicate that most thrips in tomato fields are immigrants, and that populations occurring in tomato are probably highly transient. Furthermore because tomato is a poor reproductive host, most tomato spotted wilt in tomato is a result of primary infection rather than secondary infection coming from within the crop (Puche et al., 1995). Consequently there is a pressing need to identify significant reproductive sources and characterize the dispersal behavior of *Frankliniella* thrips.

Host Location

Although tomato is not a good reproductive host for *Frankliniella* spp., it is attractive to adults of *Frankliniella* spp. Thrips use a variety of visual and olfactory cues to locate host plants (reviewed in Terry, 1997). Anthophilous thrips, such as *Frankliniella* spp. are most attracted to “flower” colors, specifically low ultraviolet (UV) reflective white, blue, and yellow (Matteson and Terry, 1992; Terry, 1997; Vernon and Gillespie, 1990). Increasing brightness of these colors increases attractiveness. Alternatively, increasing UV reflectance increases repellency. Because tomatoes have brightly colored yellow flowers, it is not surprising that they are visually attractive to adult *Frankliniella* thrips (Fig. 1). However, it is also possible to take advantage of thrips’ vision for management purposes, by using UV reflective mulches. Because of the UV reflectance, these mulches can repel thrips and inhibit them from landing on plants (Reitz et al., 2003; Stavisky et al., 2002; and discussed elsewhere in this symposium).

Interactions with Tomato Spotted Wilt Virus

TSWV has a fascinatingly complex relationship with its thrips vectors. TSWV can only be successfully acquired by larval thrips, primarily as first instars (Tsuda et al., 1996; Van De Wetering et al., 1996). *F. occidentalis* may acquire TSWV as an adult, but such individuals do not become competent vectors (de Assis Filho et al., 2004). Second instars are physiologically capable of transmitting the virus (Wijkamp and Peters, 1993), but they do not readily move from plant to plant. Therefore, transmission is essentially restricted to adults. Transmission can occur quite rapidly, often in as little as 5 minutes (Wijkamp et al., 1996).

The epidemiology of tomato spotted wilt in tomato may be critically linked to the fact that transmission times can be so brief and that tomato is attractive to adults but is not a preferred feeding host. The progression of tomato spotted wilt may be rapid in tomato as *Frankliniella* thrips feed briefly on individual tomato plants, transmit the virus, and then move on to others in a short period of time. In contrast, spread of tomato spotted wilt may be retarded on more preferred feeding hosts because adult thrips are likely to remain in residence longer on a particular plant and therefore less likely to move from plant to plant (Fig. 4).

Interspecific behavioral differences among vector species can also affect TSWV epidemiology. *F. occidentalis* acquires TSWV at a higher rate than *F. bispinosa* (Y. Avila et al., unpublished data), but field and laboratory data indicate that *F. bispinosa* is more active than *F. occidentalis* (Ramachandran et al., 2001, SRR, unpublished data). Based on this differential activity, *F. bispinosa* would move from plant to plant at a greater frequency than the more sedentary *F. occidentalis*. Consequently from a population perspective, *F. bispinosa* may account for a disproportionate amount of transmission relative to the frequency of viruliferous adults.

Effects of Behavioral Variation on Management

Interspecific differences in movement patterns can further affect management programs for thrips and TSWV. For example, an insecticide application may kill the

thrips in a field but more active and mobile species like *F. bispinosa* and *F. tritici* can rapidly recolonize that field, making it appear as if those species are not susceptible to that particular insecticide (Ramachandran et al., 2001; Reitz et al., 2003). In contrast, the more sedentary *F. occidentalis* would be slower to recolonize the same field. Such phenomena would make it appear that *F. occidentalis* is more susceptible than *F. bispinosa* or *F. tritici* to the same insecticide(s), which may not be true based on toxicity trials. Spinosad, an insecticide with a relatively short residual period, is commonly used against *Frankliniella* thrips in tomato and other vegetable crops. Spinosad significantly reduces populations of *F. occidentalis* for several days after treatment. In contrast, populations of *F. bispinosa* and *F. tritici* can be as high in plots following application of spinosad as in untreated plots (Reitz et al., 2003; Stavisky et al., 2002). However, laboratory assays with thrips derived from the same field populations show that all three species are equally susceptible to spinosad (Eger et al., 1998). These data support the hypothesis that the differential effects of spinosad seen in the field result from interspecific differences in recolonization rates rather than from differences in susceptibility to spinosad. These differences could lead to erroneous conclusions on the efficacy of insecticides.

CONCLUSIONS

To successfully manage TSWV, it is imperative to consider interactions among all three legs of the disease triangle, vector, pathogen, and host. As discussed above, the behavioral ecology of thrips vectors is crucial to the epidemiology of tomato spotted wilt. Simple differences in vector behavior can have profound consequences for the spread of TSWV. Consequently comparative studies of vector behavior and interactions with plants are the most efficient and effective approach to gaining insights into this complex pathosystem. Further comparative studies of vector behavior and interactions with plants should yield a better understanding of the dynamics of TSWV and new approaches to managing TSWV throughout the broad range of cropping systems in which it is a pest.

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Figures

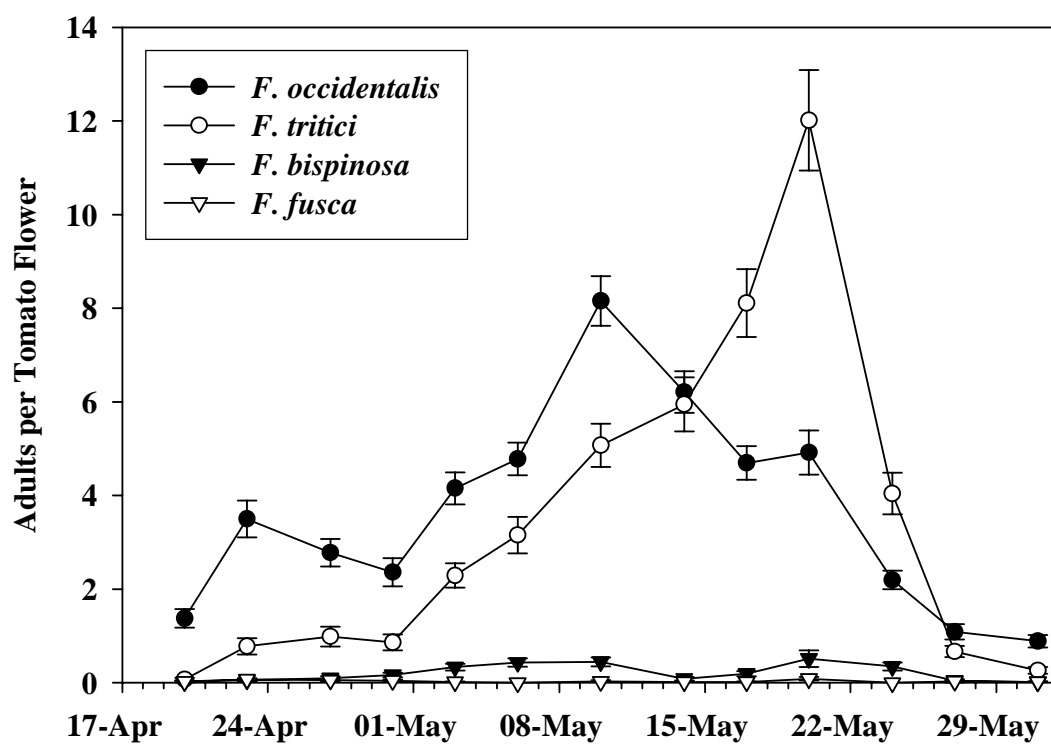


Fig. 1. Mean number of adult *Frankliniella* spp. per flower in untreated tomato during spring 2000 at Quincy, FL.

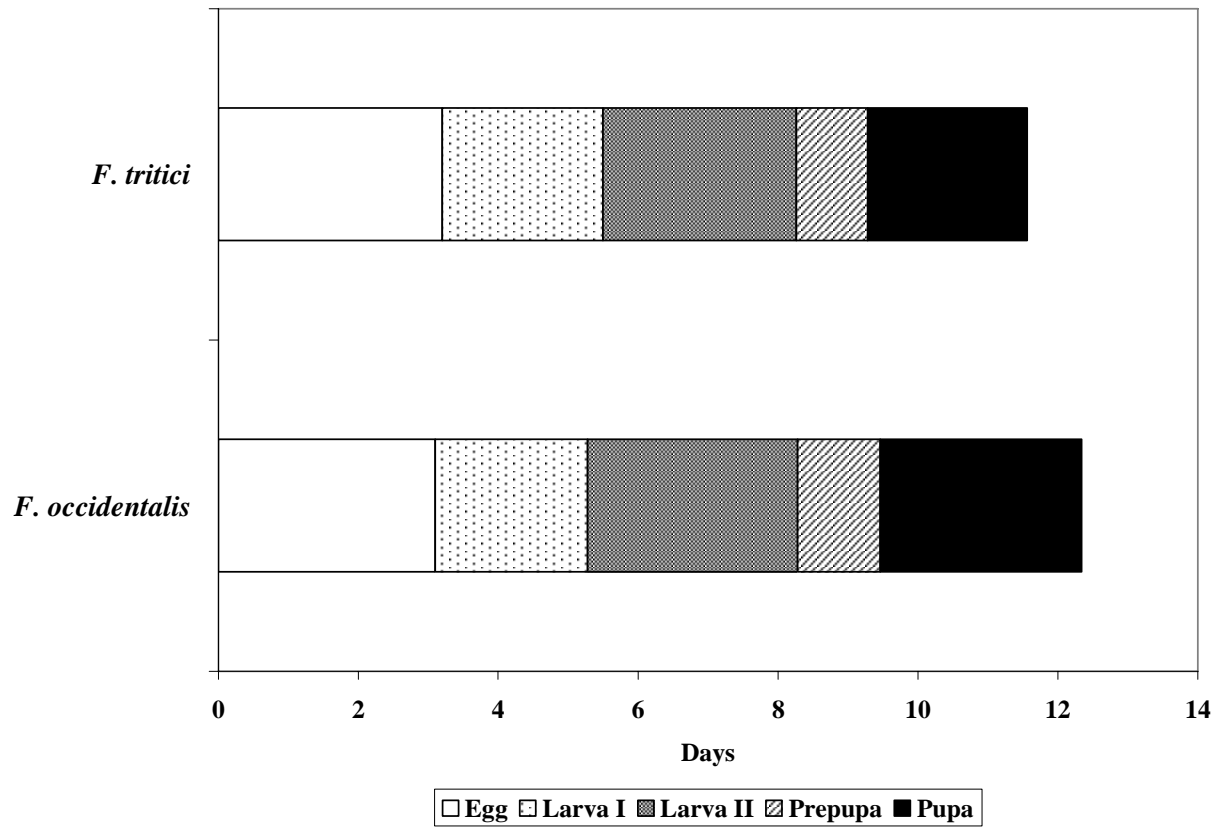


Fig. 2. Comparative development times for life stages of *Frankliniella occidentalis* (n = 40) and *F. tritici* (n = 37) females reared on green bean pods. The total development time is significantly less for *F. tritici* than for *F. occidentalis* ($F_{1, 41} = 7.33$, $P < 0.01$, one way ANOVA), with the primary difference being the duration of the pupal stage.

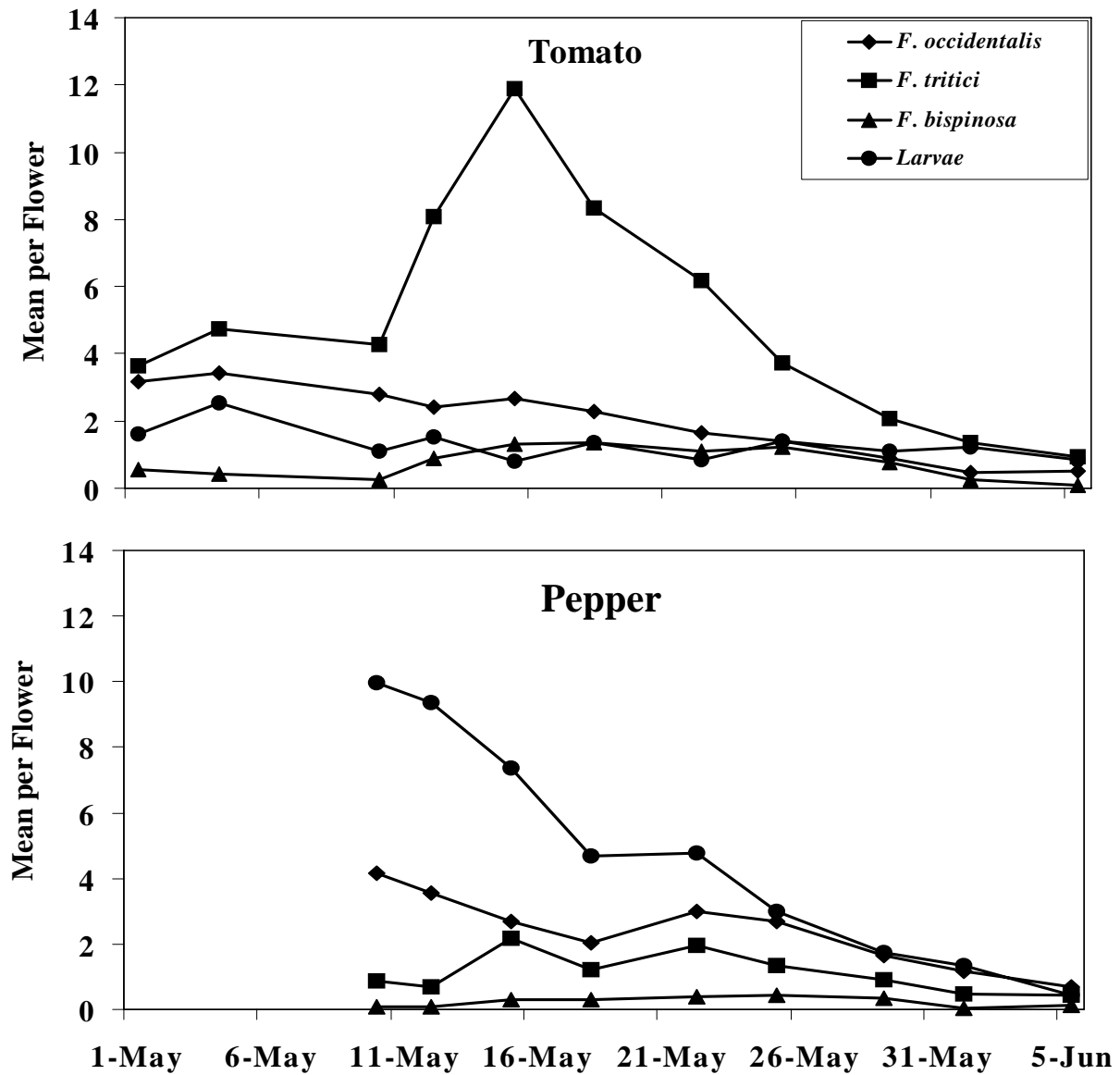


Fig. 3. Representative seasonal dynamics of *Frankliniella occidentalis* and *F. tritici* in tomato and pepper in north Florida. Data are from the spring 2000 growing season. (Modified from Baez, 2002).

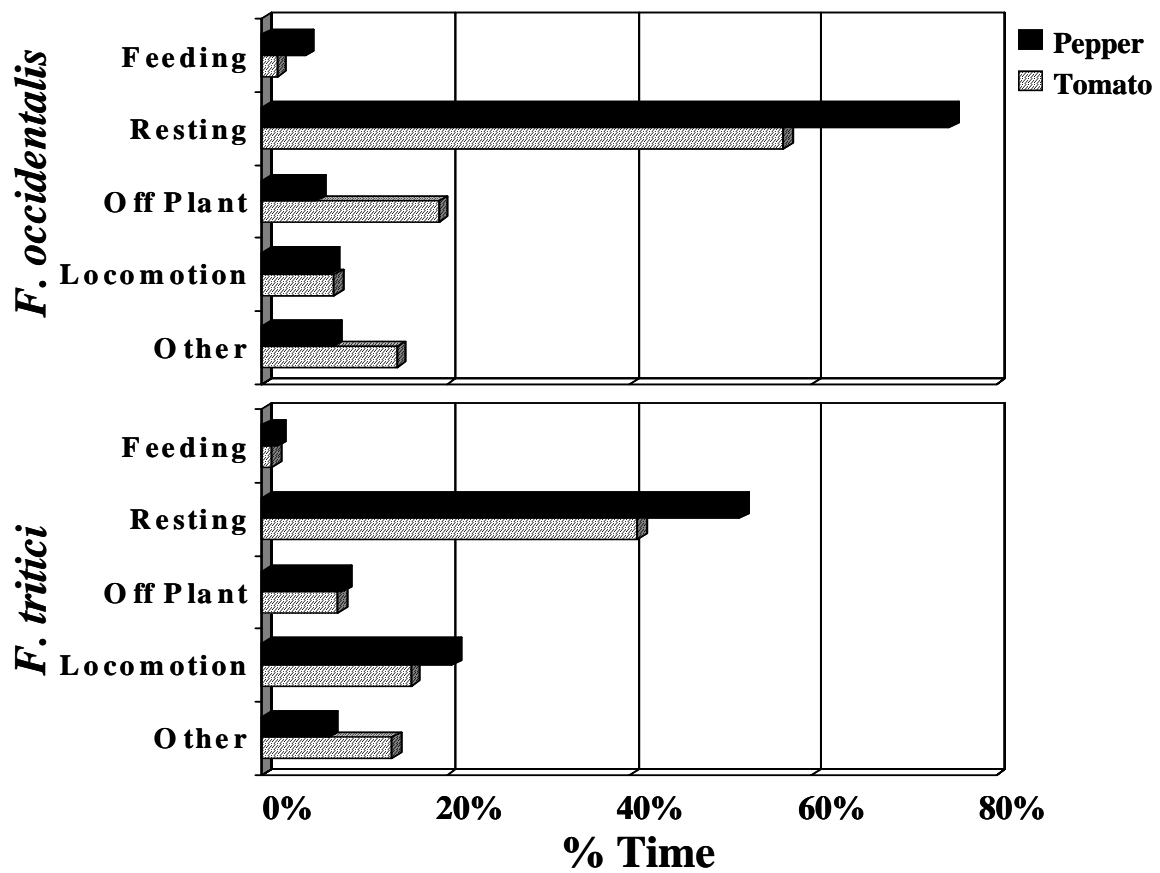


Fig. 4. Time budgets recorded for females of *F. occidentalis* and *F. tritici* on either tomato or pepper. Arenas contained a flower, flower bud and leaf of one of the host plant species. Over 95% of time spent on plant parts was spent on the flowers. Therefore, the behaviors on the three different plant parts have been summed. Only the percent of time spent in the predominant behaviors of feeding, resting on plant parts and moving, and percent of time spent not moving but off of any plant part are shown. Percent of time spent in all other behaviors are grouped as “other”.